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CITATION:

YAMAOKA, Kosaku. Feeding Behaviour and Dental Morphology of Algae Scraping Cichlids (Pisces: Teleostei) in Lake Tanganyika. African Study Monographs 1983, 4: 77-89

ISSUE DATE:

1983-12

URL:

https://doi.org/10.14989/68000

African Study Monographs, 4: 77–89, December 1983

FEEDING BEHAVIOUR AND DENTAL MORPHOLOGY OF ALGAE SCRAPING CICHLIDS (PISCES: TELEOSTEI) IN LAKE TANGANYIKA

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ABSTRACT Feeding behaviour in the natural situation and dental morphology of 13 Tanganyika species belonging to 6 genera of algae scraping cichlids were studied to understand the degree of specialization for algae feeding in relation to size. Three parameters, speed of grazing (SG), successive repeated times (SRT) and time interval of browsing (TIB), were measured to analyse the behaviour. The first two parameters were applied to 6 species of *Petrochromis*, grazers and the third one to 7 other browsing species. Among grazers, *Petrochromis polyodon* is regarded as the most adapted and *P. fasciolatus* as the least adapted to grazing diatoms off the filamentous algae. Among browsers, *Telmatochromis temporalis* has distinctive behavioural and morphological features, showing the lowest degree of adaptation. The other 6 browsing species share similar features. *Limnotilapia dardennei* and *Simochromis diagramma* show a lower degree of adaptation. *Tropheus moorei* can be regarded as the best adapted to browsing filamentous algae by shearing. *S. babaulti* and *S. marginatus* are situated between each of them. *Pseudosimochromis curvifrons* seems to diverge into browsing by cutting, not shearing. TIB can be regarded as a handling time. The validity of the "jacks-of-all-trades" hypothesis is discussed.

INTRODUCTION

During the last decade, the adaptive nature of feeding in cichlid fishes has been studied by electromyographic techniques mainly by Liem (Liem, 1974, 1978, 1979, 1980a, 1980b; Liem and Osse, 1975). These studies have revealed that the cichlids show a higher feeding versatility in artificially reared conditions than is apparent in nature. However, as noted by Bock and von Wahlert (1965) and Bock (1977, 1980), field as well as laboratory observations are important to understanding adaptations.

The Great Lakes of East Africa in which the cichlids exhibit a great diversity in feeding habits are a particularly suitable area in which to study eco-morphology. Takamura (in press) pointed out on the basis of stomach content analysis that there are two principal feeding habits in so-called Aufwuchs eaters of Lake Tanganyika: unicellular and filamentous algae feeders. The former seems to be equivalent to grazers which purposely pick up large quantities of the substratum including diatoms (Jones, 1968). The latter is equivalent to browsers which are strict herbivores that bite and tear off bits of multicellular benthic algae without (or at least rarely) taking any of the inorganic matter from the substratum (Jones, 1968). However, there have been no field observations except by Yamaoka (1982) on how Tanganyika cichlids, grazers and browsers scrape algae differently. Yamaoka (1982) compared the grazing behavour in the adult stage of five species of *Petrochromis*.

In the present paper, I will discuss the relation between feeding behaviours in nature and some dental morphology in 13 algae scraping species of six genera, to understand the degree of specialization for grazing or browsing.

STUDY AREA AND METHODS

Observations were made mainly at the northwestern rocky shore of Lake Tanganyika near Luhanga (3°31'S, 29°09'E), and subsidiarily at the rocky shore beneath the Mahale Mountains (6°05'S, 29°44'E), on the east coast of the lake from Jan. through Mar., 1980 and from July through Dec., 1981. Feeding behaviour was observed for a total of about 300 hours. The main observation site was a 400 m^2 quadrat in Luhanga (Hori et al., 1983). Most observations were carried out with the help of SCUBA to a depth of 13 m, but mainly at depths of up to 3 m.

The species studied were: *Limnotilapia dardennei* (Boulenger), *Petrochromis polyodon* Boulenger, *P. fasciolatus* Boulenger, *P. trewavasae* Poll, *P. orthognathus* Matthes, *P. famula* Matthes and Trewavas, *P. macrognathus* Yamaoka (described by Yamaoka, 1983), *Pseudosimochromis curvifrons* (Poll), *Simochromis diagramma* Günther, *S. babaulti* Pellegrin, *S. marginatus* Poll, *Telmatochromis temporalis* Boulenger and *Tropheus moorei* Boulenger. Three parameters were measured in the analysis of feeding behaviour. Two were the speed of grazing (SG) and successive repeated times of grazing (SRT) (Fig. 1a) which were applied to species of *Petrochromis* (Yamaoka, 1982). SG and SRT could not be applied to the other seven species because they did not exhibit continuous feeding, i.e., pressing the mouth against the rock surface throughout several mouth-opening and -closing reciprocation cycles, but showed rather continual browsing (nipping). After each nipping, the mouth was removed from the rock surface. The third parameter was the time interval of browsing (TIB) (Fig. 1b). Several regular continual browsings make a set of browsing behaviour. When the regularity became disordered and the duration lengthened, I regarded a set of browsing as ended. Data were collected for each set of browsing. When TIB becomes longer, one cannot discriminate it from the duration between each set of browsing. As for *Tropheus moorei* and *Pseudosimochromis curvifrons* whose TIB did not generally exceed one second, TIB shorter than one second were counted. As regards the other five species (*L. dardennei*, *S. babaulti*, *S. diagramma*, *S. marginatus*, *T. temporalis*), data for periods shorter than two seconds were used. Standard length (SL) was estimated in the water by means of approaching fishes as closely as possible with a graduated semitransparent plastic film.

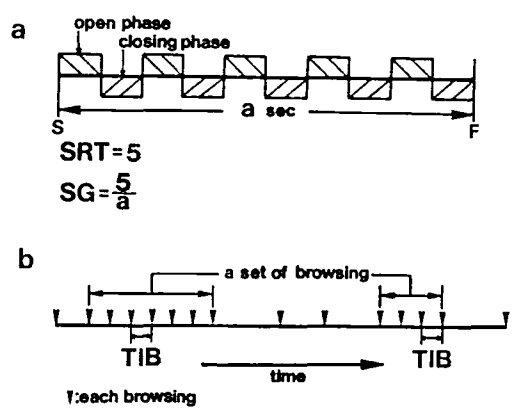

Fig. 1. Diagam showing method of measuring three parameters. a: speed of grazing (SG) and successive repeated times of grazing (SRT) which are, in this case, 5/a and 5, respectively. S, start for measure of duration defined by a touch of the mouth to rock surface. F, conclusion defined by removal of the mouth from rock surface. One open and closing phase constitutes one bite. b: time interval of browsing (TIB) is measured as the time between each browsing which is shown by the vertical arrowhead mark. Several regular continual browsings make a set of browsing.

SG, SRT and TIB of each fish were taken on the basis of 10–100, 10–223 and 9–150 observation times, respectively.

Specimens used for dissecting were collected near Luhanga. Observation and drawings were made with the camera lucida of the Wild-M7S stereoscopic dissecting microscope.

RESULTS

Grazers

As *Petrochromis* spp. feed predominantly on diatoms (Takamura, in press), they can be

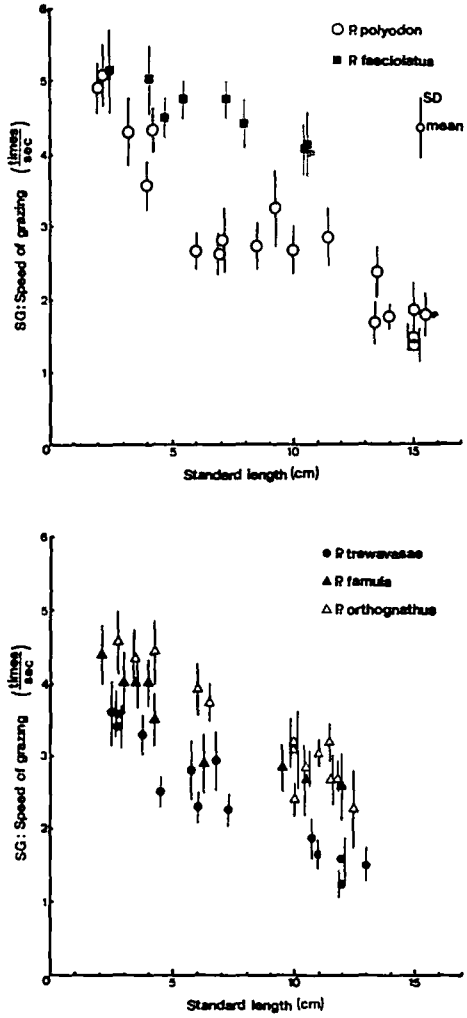

Fig. 2. Relation between standard length and speed of grazing (SG) in five species of *Petrochromis*. Mean value and standard deviation for each fish observed are given. Range of number of observations: *P. polyodon*: n = 12–48, *P. fasciolatus*: n = 10–30, *P. trewavasae*: n = 10–59, *P. famula*: n = 16–25, *P. orthognathus*: n = 10–44. P, data from plural individuals whose number of observations are less than 9 and standard lengths are similar.

classified as grazers. As shown by Yamaoka (1982), *Petrochromis* opens its mobile mouth and presses its thick lips covered with many tricuspid teeth against a rock surface. When the mouth is closed, the teeth comb diatoms from the filamentous algae attaching firmly to the rock. This behaviour is repeated a few or several times in quick or slow succession.

SG decreases with growth in every five species of *Petrochromis* (Fig. 2). There were interspecific differences in this respect. SG of *P. fasciolatus* was the fastest among all throughout the ontogenetic series. It only decreased slightly with increasing age. *P. trewavasae* grazed with the slowest speed throughout. Two individuals of *P. polyodon* about 2 cm SL displayed a faster speed which was almost the same as that of *P. fasciolatus*. Afterwards, SG of *P. polyodon* declined abruptly until the fish was about 6 cm SL. Individuals between 6 cm and 12 cm SL appeared to retain almost the same speed and those larger than 13 cm SL showed the same slower speed as *P. trewavasae*. SG of *P. orthognathus* and *P. famula* was intermediate between

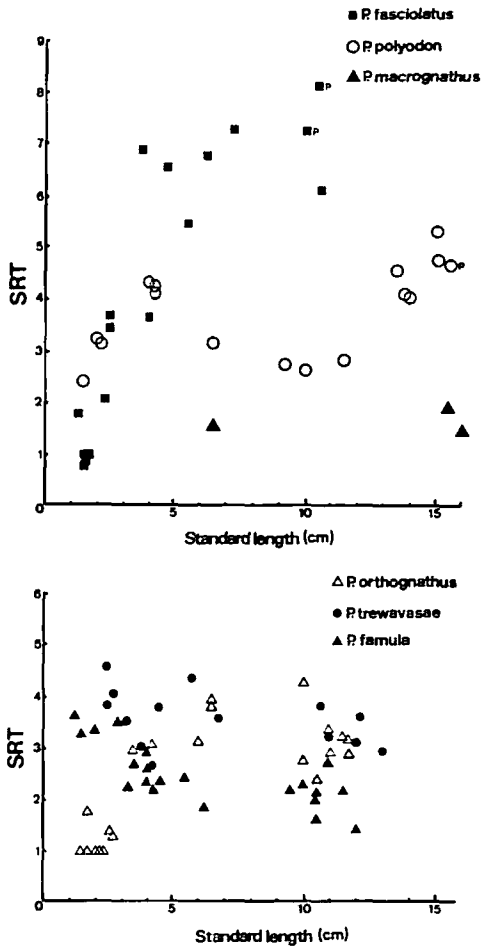

Fig. 3. Relation between standard length and successive repeated times (SRT) of grazing in six species of *Petrochromis*. Mean values for each fish observed are given. Range of number of observations; *P. polyodon*: n = 14–217, *P. fasciolatus*: n = 12–137, *P. macrognathus*: n = 25–59, *P. trewavasae*: n = 11–223, *P. famula*: n = 10–122, *P. orthognathus*: n = 11–146. Other symbols are the same as in Fig. 2.

those of *P. fasciolatus* and *P. trewavasae*. From the early stages to about 10 cm SL, *P. orthognathus* grazed faster than *P. famula*, but the difference became smaller and almost indiscernible with growth. It was impossible to measure the SG of *P. macrognathus*, because the wash prevented observation of its detailed feeding behaviour, usually at nearly vertical rock faces in the surge zone.

Fig. 3 shows the change of values of SRT in six species of *Petrochromis*. *P. fasciolatus* and *P. orthognathus* often fed with single nips while about 1.5–2 cm SL. In *P. fasciolatus* the value increased abruptly at the stage of 4–5 cm SL. Afterwards, it did not increase very much. *P. orthognathus*, however, showed a more gentle increase to the stage of 6–7 cm SL. Individuals larger than 10 cm SL tended to graze with fewer SRT. *P. famula*, *P. polyodon* and *P. trewavasae* had several SRT values even at the earlier stage. In *P. famula*, the value decreases gently to the stage of 5–6 cm SL, and afterwards it did not change much with growth. The value at the adult stage seems to be the smallest, together with that of *P. macrognathus*, among *Petrochromis* spp. For *P. polyodon*, the value for individuals of less than 2 cm SL was smaller than that of corresponding stages in *P. famula*. It increased to the 4 cm stage, then decreased to that of 10 cm SL. Afterwards, it increased again with growth. Individuals of *P. trewavasae* at the stage of 2.5 cm SL displayed the largest SRT value amongst juveniles of *Petrochromis*

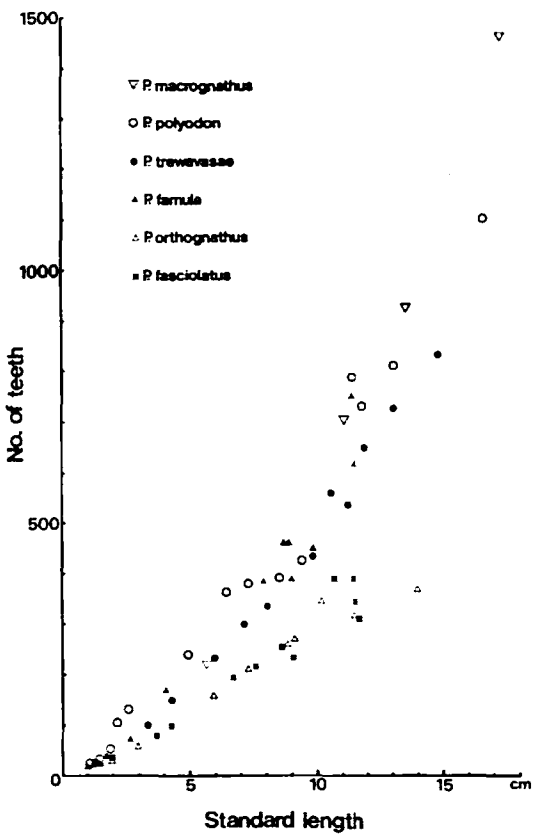

Fig. 4. Relation between standard length and total number of left upper and lower jaw teeth in *Petrochromis* spp.

spp. Its value, then, decreased but did not exhibit a specially fixed trend. In individuals larger than 11 cm, it was almost stable. *P. macrognathus*, in spite of the scarcity of data, appeared to graze with the lowest SRT value within the genus during the stage of 6.5–16 cm SL.

With regard to the number of jaw teeth at the early stages, six species could be separated into two groups; many-toothed and sparsely-toothed (Fig. 4). The former includes *P. polyodon*, *P. trewavasae*, *P. famula* and *P. macrognathus*, the latter *P. orthognathus* and *P. fasciolatus*. However, in specimens smaller than 2 cm SL it is impossible to distinguish between these two groups.

Browsers

The species studied other than *Petrochromis* spp. repeated several bites almost regularly in quick succession. They predominantly tore off multicellular filamentous algae from rocks (Takamura, in press), using bicuspid outer jaw teeth generally.

There were interspecific differences in TIB and its change with growth of the seven species (Fig. 5). TIB of *Tropheus moorei* was the shortest throughout the ontogenetic series. When the

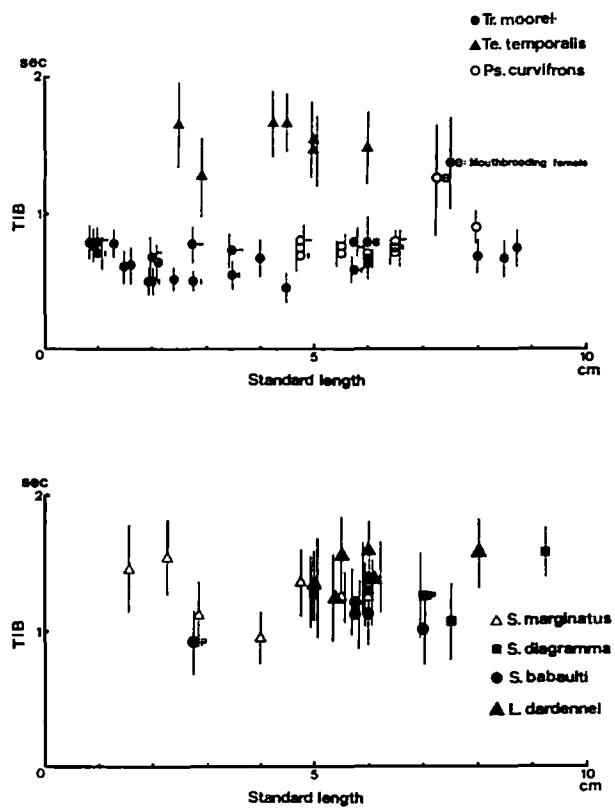

Fig. 5. Relation between standard length and time interval of browsing (TIB). Mean value and standard deviation of each fish observed are given. Range of number of observations: *Tropheus moorei*: n = 16–115, *Pseudosimochromis curvifrons*: n = 10–92, *Telmatochromis temporalis*: n = 9–65, *Simochromis marginatus*: n = 11–69, *S. babaulti*: n = 25–150, *S. diagramma*: n = 23–113, *Limnotilapia dardennei*: n = 13–115. A horizontal bar represents browsing on horizontal rock surface, a vertical bar, browsing on a vertical one. B, mouth brooding female.

adult touched the mouth to the rock surface, the rap could be heard in the water. The feeding behaviour of juveniles of 1–1.5 cm SL is already almost the same as that of the adults. TIB at this stage decreased a little to the 2 cm stage. Afterwards, it did not show a remarkable change to the stage of 4.5 cm SL, and increased a little with further growth. This species showed differences in TIB in response to the topography of the browsing site. It was shorter at the vertical or slightly overhanging rock surface than on a horizontal or slanted one (Figs. 5 and 6). In the case of the latter, when *T. moorei* browsed at the same spot as one just grazed by *P. trewavasae*, TIB tended to become shorter than when browsing at a nongrazed area (Fig. 6). This indicates that *T. moorei* can more easily browse on those parts of rocks where no sediments accumulate. The reason is that the vertical surface is unlikely to accumulate inorganic sediments and *P. trewavasae*, in the case of the horizontal or slanted surface, grazes unicellular diatoms together with inorganic debris attached to the filamentous algae (Takamura, 1983).

Females of *T. moorei* who have expanded lower parts of the head because of brooding eggs or larvae in the mouth browsed with relatively longer intervals (Fig. 5).

Pseudosimochromis curvifrons browsed with the second shortest interval. In this species, TIB looked different depending on the topography of the browsing site. It was somewhat shorter on a vertical surface than on a horizontal one (Fig. 5).

A mouth brooding female of this species browsed as slowly as did that of *T. moorei*.

Telmatochromis temporalis and *Limnotilapia dardennei*, in spite of the lack of observation on smaller individuals, appeared to show the longest TIB (Fig. 5). Three species of *Simochromis* browsed with intermediate TIB between *Pseudosimochromis* and the *Telmatochromis-Limnotilapia* group.

While browsing, *T. moorei*, *P. curvifrons* and three species of *Simochromis* usually swung the head distinctly from side to side. By contrast, *T. temporalis*, instead of swinging of the head, undulated of its rather elongate body.

Based on the morphology of outer jaw dentition in the young and adult stages, seven species could be classified into two groups: bicuspid-toothed and tricuspid-toothed (Fig. 7). The

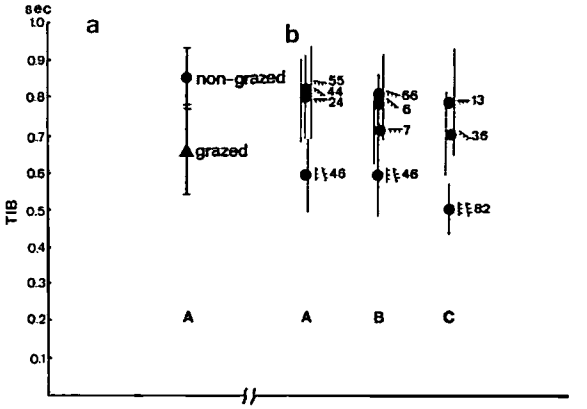

Fig. 6. Difference in TIB in response to topography in three individuals (A, B and C) of *T. moorei*. Mean values and standard deviations of TIB for each individual are given. Standard length of A and B is about 6 cm and of C about 3 cm. The feeding sites are about 1.5 m deep. a: ▲, TIB at spots just grazed by *Petrochromis trewavasae*, (n = 16); ●, TIB at non-grazed site, (n = 19); observed on 2nd Oct. 1981. b: Marks and figures on the right side denote angles of rock surface browsed and number of observations, respectively, observed on 30th Sept. 1981.

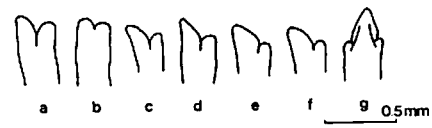

Fig. 7. Labial view of the crown of newly erupted outer jaw teeth on medial part of the left lower jaw in seven browsing species. a, *T. moorei*, (specimen used, SL: 9.87 cm); b, *P. curvifrons*, (8.94 cm); c, *S. marginatus*, (7.48 cm); d, *S. babaulti*, (6.48 cm); e, *S. diagramma*, (13.25 cm); f, *L. dardennei*, (14.23 cm); g, *T. temporalis*, (5.08 cm). Scale indicates 0.5 mm.

former includes *T. moorei*, *P. curvifrons*, *Simochromis* spp. and *L. dardennei*; the latter *T. temporalis*. All species have tricuspid inner jaw dentition.

Even within the bicuspid toothed group, there were interspecific differences in the shape of bicuspid crown (Fig. 7) and the arrangement of jaw dentition (Fig. 8). In *T. moorei*, outer jaw teeth are very densely and regularly implanted and there is almost no gap between them. The bicuspid crown develops well and a medial cusp is a little larger than a lateral one (Fig. 7). An incision between them develops moderately. On occlusion, outer teeth series of the upper jaw is situated a little anteriorily to that of the lower jaw. In *P. curvifrons*, outer jaw teeth are regularly and densely implanted, but the number of outer jaw teeth and width of jaw are smaller than those of *T. moorei*. The bicuspid crown of outer jaw teeth and the incision develop only weakly. Crowns of functioning teeth of outer series and tricuspid ones of inner

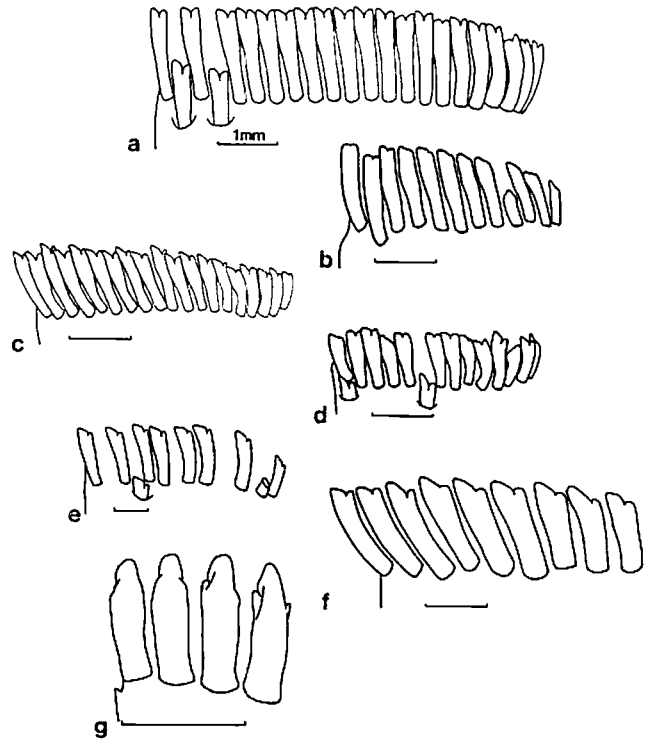

Fig. 8. Labial view of arrangement of outer jaw teeth on medial part of the left lower jaw. Right side indicates dental symphysis. Labels and specimens used as in Fig. 7. Scales indicate 1 mm.

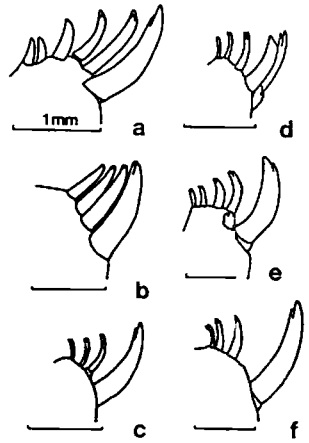

Fig. 9. Medial view of teeth implantation of the left lower jaw, showing the space between outer and inner teeth series. Labels and specimens used as in Fig. 7. Scales indicate 1 mm.

series become spatula-like teeth. On occlusion, the outer teeth series of the upper and lower jaws occlude each other, at least at the medial part of the series. The outer series of the upper jaw covers that of the lower jaw at the lateral part of the mouth. In *S. marginatus* and *S. babaulti*, the outer jaw teeth are densely implanted. The bicuspid crown develops well and the medial cusp is larger than the lateral one. The tip of the medial cusp tends to bend medially a little. The incision develops well. On occlusion, outer jaw series of the upper jaw covers that of the lower jaw. In *S. diagramma* and *L. dardennei*, there is a gap between each jaw tooth. The medial cusp of the crown is much larger than the lateral one. The incision is situated more laterally than that of *S. marginatus* and *S. babaulti*. Outer teeth series of the upper jaw covers that of the lower jaw. In *T. temporalis*, the mid cusp is plainly larger than the bilateral one and there is a wide gap between each jaw tooth. This gap is filled by the mid cusp of the opposite jaw on occlusion.

From the medial view, the arrangement of jaw dentition differs in the space between outer (first) teeth series and the second teeth series (Fig. 9). In *P. curvifrons* it is very narrow and all series are packed solidly like a single, robust teeth series functioning as one unit. As a whole, the jaw dentition looks like the beak of a bird. *Simochromis* spp. and *L. dardennei* have a somewhat widely spaced teeth. *T. moorei* is intermediate between them.

DISCUSSION

Yamaoka (1982) has suggested that in adults of *Petrochromis* a slow motion of jaws while feeding is regarded as more adaptive than a fast motion for combing off the epilithic algae in a manner analogous to an automatic rice grain thresher. The small number of jaw teeth and the fast motion of jaws in *P. fasciolatus* throughout the ontogenetic series suggest that this species may have the lowest degree of adaptation for combing off epilithic algae from the early developmental stages. On the other hand, *P. trewavasae* is superficially best adapted for this throughout its ontogenetic series.

Except in the early stages there was no remarkable difference in values of SG between *P. trewavasae* and *P. polyodon*. The difference in the early stages may be due to their habitat seg-

regation. Small individuals of *P. polyodon* graze on epilithic algae in open places in the surge zone. If SG were slower and/or the value of SRT were larger, as in *P. trewavasae*, they could only make about one bite each time, before the next wave surged back. Small *P. trewavasae* usually graze in the somewhat cryptic zone among rocks or boulders 1–2 m deep where wave action does not affect the feeding behaviour so much (Yamaoka, pers. obs.). Since that region tends to be dark, it is not very good for growth of algae. According to Hori et al. (1983), *P. polyodon*, among *Petrochromis* spp. is the most numerous and predominantly distributed over the shallow, rocky substrate region where the epilithic algae grow well. Especially younger individuals tend to be distributed over the shallower region (Hori et al., 1983). They have also demonstrated that *P. polyodon* has a lower value of inclusive mean concentration, i.e., the number of other individuals of the same and other species for an individual of species 1 per quadrat, and other subordinate species of *Petrochromis* are forced to feed in more crowded areas. Morphologically, *P. polyodon* has the longest intestinal tract among *Petrochromis* spp. (Yamaoka, 1982, in prep.). These ecological and morphological facts suggest that *P. polyodon* is more adapted to this method of feeding than other congeners. As a result, the difference of SG values between *P. polyodon* and *P. trewavasae* in the early stages can be attributable to the peculiarity of each feeding site. *P. orthognathus* shows the second lowest degree of adaptation in this respect. In adaptiveness, *P. famula* may be situated between *P. trewavasae* and *P. orthognathus* from the ontogenetic point of view.

P. fasciolatus is very sparsely distributed and large individuals of *P. orthognathus* inhabit the deeper regions in the 400 m^2 quadrat (Hori et al., 1983). Both of these species, which are regarded to have a lower degree of adaptation for epilithic algae grazing (Yamaoka, 1982), demonstrate a single bite on the rock surface in the early stages.

The inverse relation between SG and SRT of *P. polyodon* with growth is unique. Large SG and small SRT values were considered, as already mentioned, to be connected with its habitat peculiarity. The next decreasing phase in SG and increasing phase in SRT until the stage of 4–5 cm SL seems to be related to the habitat. It moved from just at the surge zone to about 0.5 m deep. At the deeper level, the direct influence of waves on feeding behaviour is small and the fish is able to browse peacefully. Next, SG becomes almost stable and SRT decreases until the stage of about 11 cm SL, and the duration of each grazing is shorter than in the preceding phase. The habitat becomes wider and deeper where dominant individuals of *P. polyodon* and *P. trewavasae* form the feeding territory (Yamaoka, 1982). Smaller, non-territorial individuals are compelled to graze for shorter durations and are chased by the territorial fish. The larger fish tend to graze pacifically with slow SG and large SRT values in the territory. Therefore, the relation between SG and SRT of *P. polyodon* seems to be determined by wave action and intra- and interspecific territoriality.

T. temporalis seems to clip filamentous algae between each lateral side of mid cusps of neighbouring upper and lower jaw teeth. Together with the characteristic undulation of the rather elongated body, this species cut the filamentous algae with longer TIB. In *T. temporalis*, filamentous algae accounted for 63% of the stomach contents (Takamura, in press). This percentage was the lowest among browsers except that of *L. dardennei* (41%) which could also be regarded as an omnivore (Hori et al., 1983). They also reported that *T. temporalis* was distributed all over the quadrat and browsed at sites made up of stones and rubble which dominant grazers and browsers did not utilize. These results indicate that *T. temporalis* is less adapted to browsing epilithic algae. However, it may be suggested that this species deviated from the other six browsers to exploit its original browsing site and method.

The gap between each jaw tooth in *S. diagramma* and *L. dardennei* seems to be less effective for browsing because some filamentous algae grasped in the mouth will likely remain un-

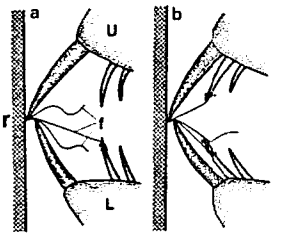

Fig. 10. Diagram showing difference of efficiency for shearing algae in response to the space between outer and inner teeth series. a: species with wide space. b: species with narrow space. U, upper jaw; L. lower jaw; f, filamentous algae; r, rock surface.

browsed. These two species, together with the other two species of *Simochromis*, have a wide space between the first and second teeth series. The tricuspid teeth of the inner series probably function to tangle the tip of filamentous algae for facilitating shearing by the bicuspid outer teeth. If this is correct, species with a wide space shear short filamentous algae with difficulty. On the other hand, species with a narrow space should shear them easily and effectively (Fig. 10). Takamura (in press) reported that 63% of the stomach contents of *S. diagramma* are filamentous algae. The percentage is also the lowest value. Only *S. diagramma* and *L. dardennei* inhabit the Ruzizi estuaries, which are covered by mud and sand, not by rocks (Kawabata and Mihigo, 1982). Of seven browsers, these two species sometimes scraped quickly with a few successive bites like grazers on a rock surface and stalk of the reed (Yamaoka, pers. obs.). These facts suggest their higher versatility and lower degree of adaptation to browsing.

Outer jaw teeth are densely implanted in *S. babaulti*, *S. marginatus*, *P. curvifrons* and *T. moorei*. This pattern seems to be effective for browsing.

The narrow space between the outer and inner teeth series of *P. curvifrons* seems to be related to the spatula-like crowns. Moreover, the outer teeth series which are made up of a smaller number of teeth of the upper and lower jaws tend to confront each other on occlusion. The tricuspid teeth of the inner series are almost spatular, which suggests not only support of the outer jaw teeth posteriorly to withstand the shock of bites but their participation in cutting algae by themselves, instead of tangling them. These facts suggest that *P. curvifrons* browses filamentous algae by cutting, not by shearing, which is performed by *T. moorei*, *Simochromis* spp. and *L. dardennei*. These species exhibit well-developed incisions of teeth crowns of outer and inner row teeth. Their dental arrangement in which the outer bicuspid teeth series of the upper jaw covers that of the lower one is advantageous for shearing (Sibbing, 1982). *P. curvifrons* has diverged a little from the other five browsing species.

The intermediate space of *T. moorei* is compensated for by the most numerous outer jaw teeth within these browsers, which form almost a straight line along the antero-ventral margin of the head. This makes it possible to browse a large quantity of algae per bite and suggests that *T. moorei* browses epilithic algae efficiently. Takamura (in press) reported that filamentous algae constituted 92% and 88% of the stomach contents of *P. curvifrons* and *T. moorei*, respectively.

The morphology of the intestinal tract, which is generally accepted as reflecting food habits, has been described by Yamaoka (unpublished). According to him, *Petrochromis* spp., grazers, have longer and more complicate intestinal tracts than browsers (*Petrochromis* type). Among seven browsing species, *T. temporalis* shows the most distinct and simplest pattern (*Telmatochromis* type) and the other six species more complex patterns, which are generally rather similar to each other, and basically the same as that of *Petrochromis* spp. (*Petrochromis*

type). Within the latter, *L. dardennei* and *S. diagramma* have a comparatively simple pattern. *S. babaulti* and *S. marginatus* have a well-developed one. These four species belong to *Petrochromis* subtype. *T. moorei* and *P. curvifrons* also show a well-developed, but slightly different pattern from each other and from those of the other five species (*Tropheus* and *Pseudosimochromis* subtypes). These facts accord well with the degree of adaptation to browsing, based on behavioural, ecological and osteological features.

One can discuss the relation between TIB and morphological features, such as jaw dentition and intestine and ecological features, such as food habits and micro-distribution. Generally, species morphologically and ecologically more specialized for browsing show a lower value of TIB. In this case, TIB can be regarded as a handling time and the lower its value, the more the species is specialized for browsing. Liem (1980b) stated that traditional parameters such as number of bites per unit time or handling time appear much too simplified and are very poor methods to apply to cichlids. This may be true for laboratory studies, in which one can use some advanced techniques, but at least for field work on Tanganyika herbivorous cichlids, the parameters adopted in the present study were suitable for the analysis of feeding behaviour.

Liem (1980a) has hypothesized that the morphologically and phylogenetically most specialized algae feeding cichlids (*Petrotilapia tridentiger*, *Petrochromis polyodon*, *Limnotilapia dardennei*, *Pseudotropheus zebra* and *Hemitilapia oxyrhynchus*) are not only remarkable specialists but jacks-of-all-trades on the bases of observation of feeding behaviour in the laboratory. Results of the present study do not support Liem's hypothesis. I have never observed feeding methods other than the orthodox one in the most specialized algae feeders: *Petrochromis polyodon*, *P. trewavasae* and *Tropheus moorei*. As far as my observations are concerned, in nature the most specialized species were remarkable specialists only, not jacks-of-all-trades, and less specialized species tended rather to have a higher versatility as exhibited in a common evolutionary trend. According to Liem (1979), the invertebrate pickers, *Eretmodus cyanostictus* and *Spathodus erythrodon*, show a far more versatile and complex pattern of feeding movements than that of any other teleost. Although Liem (1980a) did not treat *E. cyanostictus* and *S. erythrodon*, the two species seem to have the same versatility as that of the most specialized algae feeding cichlids. *E. cyanostictus* and *S. marlieri* scraped algae with SRT in nature (Yamaoka, pers. obs.). Ninety-three percent of the stomach contents of *E. cyanostictus* was made up of algae (Takamura, in press). In spite of Liem's (1979) proposal that *E. cyanostictus* and *S. erythrodon* are the invertebrate pickers, the former species belongs to algae feeders as also the latter probably does. Of seven species (*E. cyanostictus*, *S. erythrodon*, *P. tridentiger*, *P. polyodon*, *P. zebra*, *L. dardennei* and *H. oxyrhynchus*), the first five press the mouth against the rock surface throughout several mouth-opening and -closing reciprocation cycles. These five species can be regarded as scraping epilithic algae with grazing-like behaviour (Fryer, 1959; Fryer and Iles, 1972; Yamaoka, 1982, pers. obs.). *L. dardennei* also sometimes shows grazing-like behaviour on rock surface. In this way, among these seven species, mouths of six species have a close contact with the rock surface on feeding. When grazing with SRT, as there is usually a jaggedness on the rock surface, fishes must delicately adjust the movement of the dental pad to the uneven features. To perform this, a complicated muscle activity, including pronounced asymmetrical firings of muscles, is required. Therefore, intraspecific modulatory multiplicity in the feeding mechanism (Liem, 1979, 1980a, 1980b) seems to be derived from the above-mentioned demand for algae scraping on jagged rock surfaces, and not from demand for feeding on many kinds of food. It is important to emphasize that laboratory observations cannot always be applied directly to the field situation.

ACKNOWLEDGEMENTS I wish to express my heartfelt thanks to the Délégué Général and other members of the I.R.S. (Institut de Recherche Scientifique) of Zaïre, especially Director M. K. Kwetuenda, Messrs. M. Nshombo, M. M. Gashagaza and N.Y.K. Mihigo who are on the staff of the I.R.S./Uvira Station, for permission to conduct research in Lake Tanganyika and their support during my stay in Zaïre.

Prof. T. Iwai encouraged me throughout the study and gave critical comments on the manuscript. Prof. H. Kawanabe, the chief of my research team, gave me many suggestions and critically read the manuscript. Drs. M. Nagoshi and Y. Yanagisawa advised me on various aspects of the field study. Drs. G. Fryer, M. Hori and T. Kuwamura kindly revised an earlier draft of this paper and gave critical comments on it. Messrs. N. B. Mbomba, N. N. Lombola and J. Yamagiwa supported me in the field. To all these persons, I make grateful acknowledgements.

As to the data from Mahale, I greatly benefited from the cooperation of Drs. T. Narita and K. Takamura. I also thank Mr. E. Tarimo, Acting Director of the Mahale Mountains Wildlife Research Center of Tanzania, for his hospitality when I made a short visit there.

The study was partly supported by the Grant-in-Aid for Overseas Scientific Survey (Nos. 404130, 504328, 56041032 and 57043028) from the Ministry of Education, Science and Culture, Japan and by grants from the Ito Foundation for the Advancement of Ichthyology.

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